

# The first Palaeozoic rhytidosteid: *Trucheosaurus major* (Woodward, 1909) from the Late Permian of Australia, and a reassessment of the Rhytidosteidae (Amphibia, Temnospondyli)

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**SYNOPSIS.** A restudy of *Bothriceps major*, a temnospondyl from the Late Permian of Australia, has resulted in a new taxonomic assignment of the specimen. The species is returned to *Trucheosaurus* and the specimen is recognized as a rhytidosteid, rather than a brachyopid. Thus, it constitutes the first Palaeozoic record of the Rhytidosteidae, which has long been considered to be restricted to the Early Triassic. A phylogenetic analysis of all taxa previously included in the superfamily Rhytidosteioidea was performed. One monophyletic group, the family Rhytidosteidae, is recognized, but the relationships of most taxa within that clade remain unresolved.

## INTRODUCTION

In 1909, Woodward described a new Australian brachyopid taxon, *Bothriceps major*, based on a specimen collected in Late Permian deposits from the Sydney Basin (New South Wales). The genus was previously erected by Huxley (1859) for an Australian brachyopid, *B. australis*, represented by a single skull of unknown provenance (Watson 1919, 1956; Welles & Estes 1969; Warren 1997). Subsequently, Watson (1956) restudied *B. major* and referred the specimen to a new genus of brachyopid, *Trucheosaurus*, largely because 'in the few structures clearly shown in the only known specimen it differs from the type of the genus *Bothriceps* and indeed from all other known genera of the family', and also because 'the specimen is important as showing the occurrence of a typical brachyopid at an early horizon'. Subsequently, Cosgriff (1969) presented a brief description of *T. major* based on his own observation of part of the type material (MMF 12697), and also discussed the age of the specimen. Welles & Estes (1969) argued that the new genus, *Trucheosaurus*, could not be justified, so they returned the species to *Bothriceps*.

The holotype material of *B. major* consists of a poorly preserved specimen which includes the skull and a partial articulated postcranial skeleton. At present, the specimen comprises four pieces distributed in three different repositories: the skull (MMF 12697a) is in the Geological Survey of New South Wales (Sydney), the postcranial skeleton (AMF 50977) in the Australian Museum (Sydney), and the counterpart of both skull and postcranial skeleton (BMNH R3728) in the collections of The Natural History Museum, London.

The present paper is a redescription and a reassessment of the taxonomic position of *B. major* based on a re-evaluation of the entire holotype material. It was prompted during our joint study of the material in 1995 when the Australian part of the skull was further prepared, revealing an extended quadratojugal area on the left hand side. The specimen then assumed a triangular shape, with the

posterior margin apparently lacking both tabular projections and otic embayment, a morphology found in several members of the family Rhytidosteidae. A few patches of rhytidosteid ornament were also present. *Bothriceps major* is returned to Watson's available taxon, *Trucheosaurus*, and included in the family Rhytidosteidae. A preliminary phylogenetic analysis of the family Rhytidosteidae is presented and the position of the taxon discussed in a cladistic context.

## SYSTEMATIC PALAEOONTOLOGY

TEMNOSPONDYLI Zittel, 1888

Family RHYTIDOSTEIDAE Huene, 1920

Genus *TRUCHEOSAURUS* Watson, 1956

**TYPE SPECIES.** *Bothriceps major* Woodward 1909; Late Permian (Dzhulfian), Sydney Basin, New South Wales, Australia.

**DIAGNOSIS.** As for the type and only species.

*Trucheosaurus major* (Woodward 1909) Figs 1–6

- 1909 *Bothriceps major* Woodward: 319, pl. LI.  
1956 *Trucheosaurus major* (Woodward); Watson: 327–330, fig. 3.  
1969 *Bothriceps major* Woodward; Welles & Estes: 10.  
1969 *Trucheosaurus major* (Woodward); Cosgriff: 80.  
1972 *Trucheosaurus major* (Woodward); Howie: 269.  
1973 *Trucheosaurus major* (Woodward); Cosgriff: 1095–1100.  
1974 *Trucheosaurus major* (Woodward); Cosgriff: 94.  
1977 *Bothriceps major* Woodward; Chernin: 88.  
1981 *Bothriceps major* Woodward; Warren: 273.  
1997 *Bothriceps major* Woodward; Warren: 27, fig. 3.

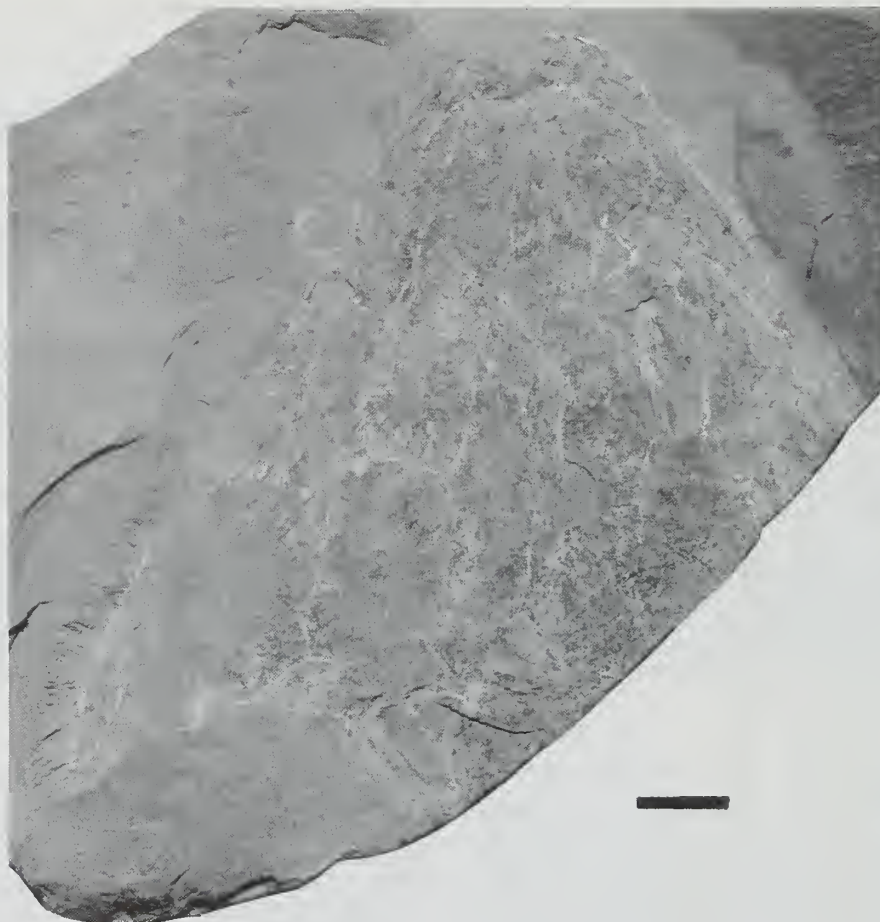


Fig. 1 *Tracheosaurus major*, holotype MMF 12697a. Skull. Scale bar represents 20 mm.

**DIAGNOSIS.** Rhytidosteid amphibian apparently lacking tabular projections and otic notch; markedly small orbits located laterally on the anterior third of the skull table; extremely anteroposteriorly elongated parietal bones, which are nearly three times the length of the frontals and apparently without pineal foramen.

**HOLOTYPE.** Skull table (MMF 12697a), the partially complete and articulated postcranial skeleton (AMF 50977), and the counterpart of both skull and postcranial skeleton (BMNH R3728).

**TYPE LOCALITY AND HORIZON.** Glen Davis Formation of the Charbon Subgroup, the lower deltaic facies of the Illawarra Coal Measures, Airly, near Capertee in the west of the Sydney Basin (New South Wales, Australia). The whole of the Illawarra Coal Measures are Late Permian (Young & Laurie 1996). The Glen Davis Formation, which is placed mid-way through the Illawarra Coal Measures (McMinn 1985), contains the palynomorph *Microreticulatisporites bitriangularis*, the index form for the base of the APP5.2 Interval Zone (Burger *et al.* 1992), making it middle Dzhulfian. This Dzhulfian correlation for the middle part of the Illawarra Coal Measures was confirmed in the most recent survey of evidence for the placement of the Permo-Triassic boundary in Australia (Foster *et al.* 1997).

#### DESCRIPTION

*Skull.* As mentioned above, the specimen is only preserved as a thin layer of bone on two slabs (part and counterpart). Although obvi-

ously part and counterpart of the same specimen, the two halves do not meet cleanly when fitted together as several millimetres of the bone is missing in places.

Determining sutures was difficult as little detail remains, perhaps because the specimen was preserved in a torbanite. The clearest sutures are in the area of the left tabular, postparietal, supratemporal, parietal, postfrontal and postorbital. The other sutures were delineated following the pattern of the bone radiation, although in the anterior snout region sutures remain fairly unclear. Suture lines were traced with chalk on the part and counterpart (Figs 1, 2) and the specimens drawn (Figs 3, 4). The drawings were then superimposed and the skull redrawn as a composite (Fig. 5). The main problem encountered during our restoration was determining the position of the orbits, which have been restored in the only possible place. The nostrils are marked by raised areas. Apparent ornamentation preserved is faint but seems to show a delicate and smooth spider-web pattern with small nodes on the ridges.

The skull table is nearly straight sided, with the posterior margin lacking both tabular projections and otic embayment. The orbits must have been very small, and located laterally on the anterior third of the skull table. There is no sign of a pineal foramen. A striking feature of the specimen is the extremely anteroposteriorly elongated parietal bones, which are nearly three times longer than the frontals. Apparently, there is no lachrymal bone.

Part of the occiput is visible behind the posterior border of the





**Fig. 2** *Trucheosaurus major*, holotype BMNH R3728. Skull. Scale bar represents 20 mm.

skull table, presumably owing to the dorso-ventral compression of the specimen. A slender left paroccipital process is the best preserved part of the skull. It shows a clear tabular-exoccipital suture close to the area of the exoccipital condyle. Part of the descending portion of the left postparietal is also preserved. Posteriorly to the postparietals, a layer of bone is present and presumably could be either part of the palate (? parasphenoid) or part of the pectoral girdle (? interclavicle). It has been omitted from the figures but can be seen in the photographs (Figs 1, 2).

On the posterior left corner of the skull, a fragment of bone projects behind the putative quadratojugal. It either represents part of an extension of the quadratojugal or is part of the mandible. In Fig. 5, we have restored it as a quadratojugal.

*Postcranial skeleton.* Parts of the right fore and hind limb and at least 31 presacral and postsacral centra are preserved, with accompanying ribs (Fig. 6).

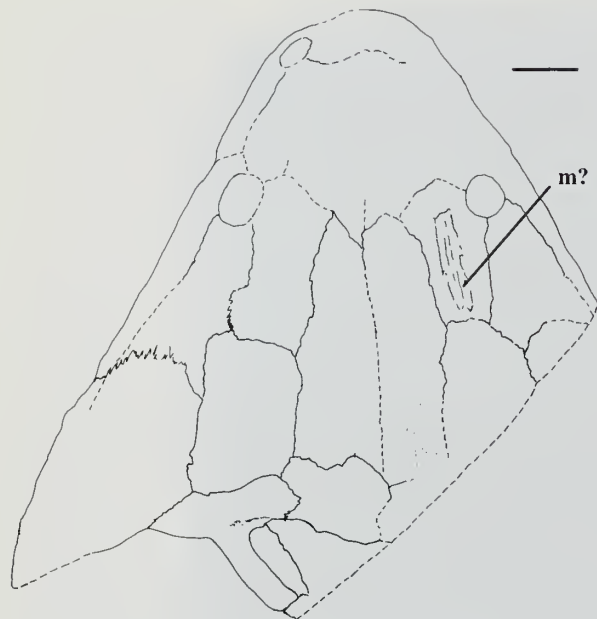
The condition of the vertebrae is such that they are most easily counted by means of the clearly defined ribs. In the anterior part of the column the section is frontal, with both left and right ribs from 21 centra preserved. More posteriorly, a flake of torbanite containing 5 ribs is missing from the right side. Following this,

the section changes so that it preserves part ribs, only, on the left and seven apparent centra with accompanying neural arches on the right. Next are three structures which resemble swept back neural spines from a tail fin with the final two vertebrae represented by poorly defined centra. The column is certainly rhachitomous in the caudal region but could be rhachitomous or stereospondylous more anteriorly.

The ribs themselves are shorter than usual for temnospondyls. In the anterior part of the column they are curved but the curvature is not preserved posteriorly. No indication of uncinat processes is present on any rib.

The humerus, radius and ulna of the right fore limb are partially preserved close to their expected position, as are several other small displaced elements. Two long bones either side of the vertebral column in this area may be the remains of a displaced left fore limb or partial pectoral girdle elements. The right hand element was labelled 'x' by Woodward (1909).

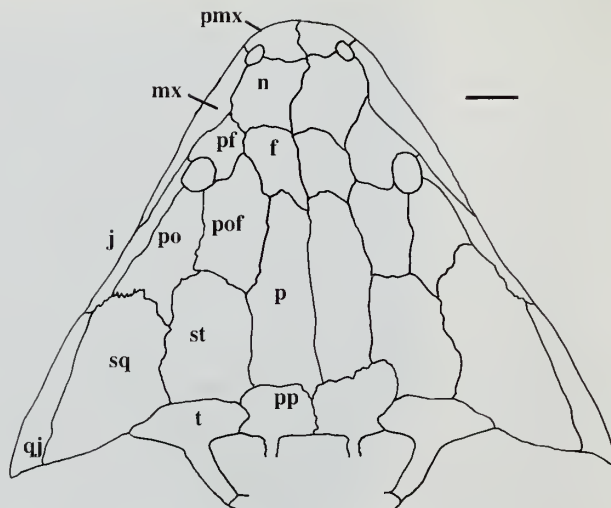
More posteriorly, several patches of bone are preserved on the right and may be the tibia and fibula of both hind limbs as well as some metapodials. There is no sign of the femora.



**Fig. 3** *Trucheosaurus major*, holotype MMF 12697a. Diagram of skull from Fig. 1. Scale bar represents 20 mm. m?, possible mandibular fragment.



**Fig. 4** *Trucheosaurus major*, holotype BMNH R3728. Diagram of skull from Fig. 2. Scale bar represents 20 mm.



**Fig. 5** *Trucheosaurus major*. Drawing of the skull incorporating only those parts preserved on MMF 12697 and BMNH R3728. No attempt has been made to correct probable flattening of the skull or to speculate on the original shape of the occiput. It is unlikely that the paroccipital process of the tabular and exoccipital protrudes posteriorly in the undistorted specimen. Scale bar represents 20 mm. f, frontal; j, jugal; mx, maxilla; n, nasal; p, parietal; pf, prefrontal; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; qi, quadratojugal; sq, squamosal; st, supratemporal; t, tabular.

## PHYLOGENETIC ANALYSIS

The family Rhytidosteidae was erected by Huene (1920) for *Rhytidosteus* and *Peltostega*. Later, Cosgriff (1965) created the superfamily Rhytidosteoidea for the Rhytidosteidae and the monogeneric family Laidleridae (Kitching 1957). Subsequently, Cosgriff & Zawiskie (1979) removed the Laidleridae and erected a new rhytidosteid family, the Indobrachiopidae, for those members of the Rhytidosteidae with rounded, as opposed to triangular, skulls. Because they were unable to distinguish the families Rhytidosteidae and Indobrachiopidae except on the basis of skull outline, Warren & Black (1985) returned the members of the Indobrachiopidae to the Rhytidosteidae. Shishkin (1994) re-erected the Rhytidosteoidea, including in it the Rhytidosteidae and Peltostegidae. More recently, Warren (1998) restricted the superfamily to the Rhytidosteidae and Laidleridae.

The purpose of this preliminary analysis is to provide a hypothesis for the relationships among rhytidosteids and determine whether more than one monophyletic group is represented. Nearly all those characters used in the different revisions mentioned above were considered. Nevertheless, the triangular shape of the skull, although it was used in all previous diagnoses of the family, was not included as it was not possible to define discrete states for this character, especially in the case of incomplete material.

The following rhytidosteid taxa were used in the analysis: *Rhytidosteus capensis* (Owen 1884, Cosgriff 1965), *Peltostega* sp. (Nilsson 1946), *Laidleria gracilis* (Kitching 1957, Warren 1998), *Indobrachiops panchetensis* (Heune & Sahni 1958, Cosgriff & Zawiskie 1979), *Deltasaurus kimberleyensis* (Cosgriff 1965), *Rewana quadricuneata* (Howie 1972), *Derwentia warreni* (Cosgriff 1974), *Arcadia myriadens* (Warren & Black 1985), *Boreopelta vavilovi* (Shishkin & Vavilov 1985), *Mahavisaurus* sp. (Lehman



Fig. 6 *Tracheosaurus major*, holotype AMF 50977. Postcranial skeleton. Scale bar represents 50 mm.



1966, Cosgriff & Zawiskie 1979), *Pneumatostega potamia* (Cosgriff & Zawiskie 1979), *Acerastea wadeae* (Warren & Hutchinson 1987) and *Trucheosaurus major*. The lydekkerinid taxa *Lydekkerina* (Parrington 1948) and *Chomatobatrachus* (Cosgriff 1974) and the family Trimerorhachidae (Broom 1913, Olson 1955) were considered as outgroups, taking into account previous cladistic analyses of the Temnospondyli (Milner 1990, 1991). All terminal taxa used in the analysis were examined by one or both of the authors. The taxon-character state matrix (Table 1) and character list are included in the Appendix.

**DISCUSSION.** The incorporation in the analysis of several taxa represented by poorly preserved specimens greatly increased the instability of the resultant cladogram, and thus the number of equally parsimonious trees. Under these circumstances, four taxa were excluded from the analysis, reducing the number of terminals to twelve. Taxa excluded were: *Mahavisaurus* sp., *Pneumatostega potamia*, *Acerastea wadeae* and *Trucheosaurus major*, and their relationships are discussed separately. Accordingly, the phylogenetic results are based on an analysis of 18 characters and 12 terminal taxa, using Swofford's (1993) PAUP 3.1. The branch-and-bound search algorithm resulted in 51 equally-parsimonious trees with a tree length of 23 steps (CI = 0.83 and RI = 0.89). Fig. 7 depicts the strict consensus tree, showing the consistent nodes among the 51 trees.

The monophyletic group (*Indobrachyops* + (*Boreopelta* + *Derwentia* + *Laidleria* + *Peltostega* + (*Rhytidosteus* + *Deltasaurus*) + *Rewana* + *Arcadia*)), that we consider the family Rhytidosteidae (Fig. 7, node 1), is supported by the following eight unequivocal synapomorphies: orbits located close to the skull margin (1); otic notch reduced or absent (3); tabular horns reduced or absent (4); straight posterior margin of the palate (7); otic flange absent (8); 'pockets' on the parasphenoid absent (11); cultriform process of the parasphenoid broad and flat (14) and exoccipital condyles horizontally elongated (16). Two further derived character states of this clade are: the presence of a 'twisted' quadrate ramus of the pterygoid (10), and a reduced palatal tooth row (17), although the former reverses in *Derwentia* and the latter reverses in *Peltostega* and *Laidleria*. The derived condition of character 18 (presence of shagreen on all bones of the palatal series) has long been used as a diagnostic family

character (Cosgriff & Zawiskie 1979, Warren & Black 1985, Warren & Hutchinson 1987, Shishkin 1994). In the present analysis, this derived character state justifies a more inclusive group which includes the Tasmanian 'lydekkerinid' *Chomatobatrachus*. Moreover, among rhytidosteids, the shagreen is reduced in *Derwentia* and apparently absent in *Laidleria*. The condition present in *Indobrachyops* for characters 7, 8 and 16 is unknown, and their derived states might justify a less inclusive group excluding *Indobrachyops*. Within Rhytidosteidae, *Indobrachyops* is the sister group of an unresolved clade which includes all the remaining rhytidosteid taxa: (*Boreopelta* + *Derwentia* + *Laidleria* + *Peltostega* + (*Rhytidosteus* + *Deltasaurus*) + (*Rewana* + *Arcadia*)) (Fig. 7, node 2). This monophyletic group is justified by two unequivocal derived character states: skull sculpture with nodules or pustules (5) and lachrymal bone absent (6), although the condition present in *Boreopelta* and *Peltostega* for the latter is unknown. Another synapomorphy of this clade is equivocal: the condition of a contact between the palatine and vomer lateral to the choana (15), which is unknown in *Rewana*, *Boreopelta* and *Peltostega*, and reverses in *Derwentia* and *Arcadia*. Within the clade, the sister-taxon relationship between the South African *Rhytidosteus* and the Australian *Deltasaurus* (Fig. 7, node 3) is justified by the derived condition of characters 12 (exoccipital-ptyergoid suture visible in palatal view) and 17 (palatal tooth row absent). Also, the Australian taxa *Rewana* and *Arcadia* form a clade (Fig. 7, node 4), justified by the presence of a strikingly low ascending ramus of the pterygoid (9) and the presence of the quadrate condyles well behind the occipital ones (13). It is important to remark that the Australian taxa *Arcadia*, *Rewana* and *Derwentia* share the derived condition of character 2 (the orbits in the anterior half of the skull table); however, as the presence of this condition is unknown in some of the members of the in-group (*Boreopelta* and *Peltostega*), it appears in the analysis as an equivocal synapomorphy of the (*Rewana* + *Arcadia*) clade.

Although not included in the analysis, the taxa *Mahavisaurus*, *Pneumatostega*, *Acerastea* and *Trucheosaurus* are considered rhytidosteids and in a more derived position than *Indobrachyops*. This position is supported by the presence in those taxa of a skull sculpture with nodules or pustules, and the absence of lachrymal bones. Both *Acerastea* and *Trucheosaurus* appear to be more closely related to the other Australian taxa through the presence of the orbits in the anterior half of the skull, a condition especially marked in

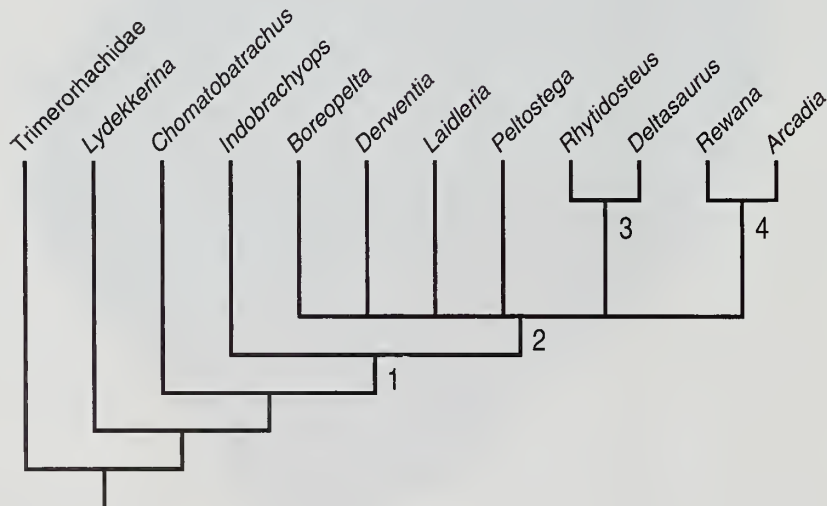


Fig. 7 Strict consensus cladogram of 51 equally parsimonious trees.

*Trucheosaurus*, and the position of the quadrate condyles behind the occipital ones, visible only in *Acerastea*.

The lack of resolution of most of the generic relationships in the analysis performed herein is apparently due to both the low number of informative characters and the amount of missing entries, which contribute substantially to the instability and poor resolution of the resultant cladogram (Novacek 1992). This result reflects the lack of consensus among investigators concerning the taxonomic validity and content of Rhytidosteioidea and its included families, a problem which has been debated over the last thirty years (see above). This situation strongly indicates that a redescription and further preparation of some specimens is needed, and in many cases the discovery of new, more complete material would improve the resolution of the analysis. Nevertheless, and as a result of the present analysis, most of the Australian taxa (*Arcadia*, *Rewana*, *Acerastea*, *Trucheosaurus*, and *Derwentia*) appear more closely related than they are to other members of the family. The only exception is the Australian taxon *Deltasaurus*, which appears as the sister-taxon of *Rhytidosteus*, from the South African Karoo.

The fact that *Trucheosaurus* is considered here to be a rhytidosteid taxon rather than a brachyopid, constitutes the first Palaeozoic record of Rhytidosteidae, a family which has long been considered to be restricted to the Early Triassic (Scythian) and because of this used in a biostratigraphic sense (Cosgriff 1969, 1984; Shishkin 1994). Conversely, Brachyopidae no longer has a Permian representative and is thus restricted to the Mesozoic. A second brachyopid, *Bothriceps australis*, was considered to be Permian but only because of its taxonomic relationship with *Trucheosaurus major*, and is most likely Triassic (Warren 1997).

When a phylogenetic hypothesis is combined with the observed fossil record of the terminal taxa, stratigraphic separation between sister-taxa demands substantial range extensions beyond those predicted by the observed stratigraphic record ('ghost lineages' of Norell 1992). Thus, the age of *Trucheosaurus* and its position on the cladogram extend the rhytidosteid diversification and preceding nodes into the Late Permian. Equally, if a more inclusive cladistic analysis of temnospondyls is considered (e.g. Milner 1990), the resultant calibrated phylogeny (Norell 1992) suggests that the phyletic diversification of Mesozoic temnospondyls ('stereospondyls') occurred earlier than indicated by the fossil record. The implication is that the apparent radiation of taxa in the Early Triassic was an extension of a Late Permian event, which probably took place in Gondwana as the earliest and most diverse of the Triassic temnospondyls faunas occur in that area. Therefore, the seeming abruptness of the Permo-Triassic temnospondyl turnover (Milner, 1990: fig. 15.3) might be both an effect of the lack of recent revisions of the known temnospondyl record and its interpretation relative to testable phylogenetic patterns, and a taphonomic artifact. The taphonomic effect may result from the absence of preserved temnospondyl-bearing sequences in the Late Permian, or the preservation of fauna from selected sequences only, as appears to have been the case in South Africa.

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## APPENDIX

### Character List for Table 1

- Position of the orbits I. The position of the orbits in relation to the skull margins: close to the skull midline (0); close to the skull margin (1).
- Position of the orbits II. The position of the orbits in relation to the skull table length: approximately in the middle (0); in the anterior half of the skull table (1).
- Otic notch: incised (0); reduced or absent (1).
- Tabular horns: well developed and posteriorly projected (0); reduced to a broad based triangle or absent (1).
- Sculpture: 'normal' ridge-grooved pattern without pustules or nodules on the junctions (0); spider-web pattern with nodules or pustules on the junctions (Cosgriff & Zawiskie 1979) (1).
- Lacrimal bone and lacrimal flexure of infraorbital sensory canal: present (0); absent (1).
- Posterior margin of the palate embayed (0); almost straight (1).
- Pterygoid otic flange (= oblique ridge): present (0); absent (1).
- Pterygoid ascending ramus. In those pterygoids without an otic flange, the ascending ramus is a thin lamina that runs along the dorsal surface of the quadrate ramus of the pterygoid and across the corpus: extremely low (1); not extremely low (2).
- Pterygoid quadrate ramus: evenly curved from the horizontal to the vertical plane throughout its length (0); horizontally oriented proximally and vertically oriented distally so it appears twisted (1).
- Ventral depressions on the parasphenoid corpus ('pockets' of Watson 1962): present (0); absent (1).
- Exoccipital-ptyergoid suture: not visible in palatal view (0); visible in palatal view (1).
- Quadrate condyles: well behind the occipital condyles (0); in the same transverse line as the occipital condyles (1).
- Cultriform process of the parasphenoid: narrow (0); broad and flat (1).
- Vomer-palatine contact external to the choana so the maxilla is excluded from its border: absent (0); present (1).
- Exoccipital condyle articular surface: rounded (0); oval and horizontally elongated (1).
- Palatine tooth row: continuous over the palatine series (0); reduced, so it is only partially present on some of the palatal bones (1); absent (2).
- Shagreen: reduced so it appears on some of the palatal series only, not including the tooth bearing bones (0); on the palatal series including the tooth bearing bones (1).

**Table 1** Taxon-Character state matrix. The matrix includes 12 taxa and 18 characters. Data missing as a result of lack of preservation or because the state is unknown is coded as '?'. Data unknown but as a result of transformation is coded as '-'. The data matrix was subjected to parsimony analysis using PAUP branch-and-bound option.

TAXA	CHARACTERS																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Trimerorhachidae</i>	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	?	0	0
<i>Lydekkerina</i>	0	0	0	0	0	0	0	0	-	0	0	0	1	0	0	0	0	0
<i>Chomatobatrachus</i>	0	0	0	0	0	0	0	0	-	0	0	0	1	0	0	0	0	1
<i>Rhytidosteus</i>	1	0	1	1	1	1	1	?	?	?	1	1	1	1	1	1	2	1
<i>Pelostega</i>	1	?	1	1	1	?	1	1	2	1	1	0	1	1	?	1	?	?
<i>Laidleria</i>	1	0	1	1	1	1	1	1	2	1	1	0	1	1	1	1	1	0
<i>Indobrachyops</i>	1	0	1	1	0	0	?	?	?	1	1	0	1	1	0	?	1	1
<i>Deltasaurus</i>	1	0	1	1	1	1	1	1	2	?	1	1	1	1	1	?	2	1
<i>Rewana</i>	1	1	?	?	1	1	1	1	1	1	?	?	?	1	?	1	1	1
<i>Derwentia</i>	1	1	1	1	?	1	1	1	2	0	1	0	1	1	0	1	1	0
<i>Arcadia</i>	1	1	1	1	1	1	1	1	1	1	?	?	0	?	0	1	1	1
<i>Boreopelta</i>	1	?	1	1	1	?	1	1	2	1	1	0	1	1	?	1	?	1